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THE EVOLUTION OF THE MARINE COTTIDAE OF CALIFORNIA WITH A DISCUSSION OF THE GENUS AS A SYSTEMATIC CATEGORY

By Rolf L. Bolin

In my recent review of the cottid fishes of California (Stanford Ichthyol. Bull., vol. 3, no. 1, 1944) genera were used which, while hardly Linnaean in scope, were not predominantly monotypic. The tendency on my part to assign more than one species, and in fact sometimes half a dozen species or even more, to a single genus appears to be considered by some of my friends as an atavistic trait; they view with alarm the grouping of related species and seem to consider my actions as a disservice to science. My personal opinion is that my presentation represents a definite advance over the system previously used and I should like an opportunity to explain my point of view to my colleagues who have, without much question, accepted the American tradition of systematic splitting. This tradition has achieved unchallenged respectability since the most eminent American ichthyologists of the last hundred years, such men as Gill, Jordan and Hubbs, have accepted and advanced it. In spite of the weight of such authority, I dare to raise an anguished and dissenting voice in a plea for the retention of the genus as a systematic category of some value and meaning.

In order to explain my point of view I should like to discuss the evolution of the California Cottidae. The tracing of the evolutionary patterns within this family will indicate the type of reasoning upon which my conception of the genus is based.

Most ichthyologists will agree that the family Scorpaenidae is the most generalized group of the order Scleroparei. It contains those fishes whose characters probably approximate most closely those of the ancient ancestral stock from which the modern, highly divergent families of the order were originally derived. Apparently the fishes of the family Cottidae are direct and somewhat more modified derivatives of this ancestral stock and, if this assumption is correct, we may postulate the primitive cottid as a fish somewhat similar to the more primitive scorpaenids. It probably was a slightly compressed and heavy-bodied form with a rather large head which bore some spines, at least four being found on the preopercle. Teeth occurred on the vomer and palatines as well as on the premaxillaries and dentaries. Four complete gills were present and the slit behind the last one was extensive, while the gill membranes, although probably joined to each other, were free from the isthmus. The soft dorsal and anal fins were comparatively short,

and the two dorsals were joined by a broad membranous connection. Five rays occurred in the pelvics and split rays characterized all of the fins except the spinous dorsal. The body was probably covered by normal but strongly ctenoid scales and only a few cirri were present. The anus was located only a short distance in advance of the anal origin and no specialized intromittant organ had been developed in the male. Additional characters might readily be ascribed to the ancestral form, but the ones listed here are among those most easily noted without dissection and, having been widely used in classification, will serve for the purposes of the present discussion. By the retention of some of the features in their primitive state and the modification of others, the genera of the family have become differentiated. Almost every genus is primitive in some regards and specialized in others.

It should be noted that the primitive nature of many of these characters is indicated by ontogenetic changes. The primitive condition is found in juveniles of some species and modifications with advancing age evidently recapitulate the phylogenetic changes and provide the intermediate stages which have been suppressed in other forms. Thus, in progressively older specimens we may note a marked change in the body form in Scorpaenichthys and Hemilepidotus, a reduction of scales in Hemilepidotus and *Clinocottus analis,* and an advance of the anus in Nautichthys and Orthonopias. On the other hand, in the case of some characters, such as the occurrence of split rays in the various fins, the juveniles provide no clue as to the ancestral condition. The rays are simple in all juveniles and it is only in larger specimens that they become branched. The tendency toward branching has been suppressed in many forms, first in the pelvics, then in the pectorals, and finally in the dorsal and anal fins. Only an examination of the adults can determine whether the various species retain the primitive split rays or not and, indeed, it is only by examination of other less specialized families that we may postulate the split rays as primitive.

It might seem that, given a fair idea of the characters of the ancestral form, the task of tracing the mutual relationships of the modern cottids should be easy. However, the investigator is very frequently confronted by the phenomenon of convergent evolution which confuses the problem with conflicting evidence. It imposes upon him the necessity of deciding whether the presence of similar features in two or more forms is or is not due to close common inheritance.

Convergence apparently may be due to either similar environments or to inherent tendencies which are in no way associated with the environment. The molding effect of the environment, whether resulting directly in genetic changes or acting as a selective agency in preserving random mutations, is well recognized. The inherent potentiality of convergent evolution has, on the other hand, been given comparatively scant attention. The fishes discussed in this paper provide a character which brings the problem into sharp focus. In the family Cottidae a number of species have developed penes. These are often of remarkable size and considerable complexity. They are conspicuous structures which at first glance appear to be strong evidence of the close relationship of all species which possess them. The evidence of several other less striking characters, however, leaves no doubt that a classification based on the penes alone would greatly distort the evolutionary picture. In a case like this we are evidently confronted with the inheritance throughout the family of *a tendency to develop a structure, a potentiality of mutation* in a certain direction. One of the genes is apparently of an unstable nature. In its complex molecular structure there may be, possibly, some chemically weak spot where, conditions being favorable, an atom may readily be added or subtracted or replaced by a different one, resulting always in a similar somatic modification. Evidently the occurrence of such conditions and the resulting bodily changes are not rare in

geologic time. The same type of modification recurs here and there throughout the Cottidae. It is simply extraspecific or extrageneric recurrent mutation, being much the same as intraspecific recurrent mutation and differing only in added or superimposed modifications due to the previous specific or generic differentiation of the mutating organisms. It may also be pertinent to remark that such extraspecific recurrent mutation is not confined within the limits of the family by any means. Inheritance of the tendency to develop cirri in particular places or to advance the anus from its normal position is shared with other families of the order and even with other orders. Such convergence often results in several characters each suggesting different relationships and each seemingly of considerable importance. The investigator is then driven to choosing between characters. He can be fairly sure of himself only if he finds a number of substantiating characters to outweigh numerically the misleading ones. If this is impossible, he must, unfortunately, rely upon his intuition.

With this brief explanation of some of the difficulties involved, and a frank admission of the subjective nature of some of my conclusions, I present a diagram of the interrelationships of the genera of marine cottid fishes known from California. There is no doubt that certain sections of the diagram, particularly the left-hand portions, are replete with errors but I offer no apologies for its imperfections since I consider it to be a much more accurate presentation than is possible by the mere listing of species in print.

The ancestral cottid stock evidently possessed so many potentialities for mutation which were repeatedly expressed in divergent evolutionary lines that the interrelationships of the early branches of the cottid family tree are obscured by a mass of contradictory evidence and can only be surmised.

Among the most conservative of the cottids is *Scorpaenichthys marmoratus*, the single representative of its genus and the end-product of a sterile evolutionary line. It retains a body form close to the one postulated for the ancestral type and juveniles are even more primitive in this regard than are the adults. Teeth are retained on the vomer and palatines, four gills are still present with a well developed slit behind the last one and the gill membranes are free from the isthmus. The dorsal fins are primitive in being strongly connected by membrane, the pelvics have their full complement of five rays and branched rays occur in all of the fins. The anus is not advanced nor has the anal papilla developed into a penis in the male. Opposed to these conservative features a number of new modifications may be noted. Among these are a moderate reduction of the preopercular spines, the fourth or lowest one being entirely unrepresented, while the third one becomes obsolescent in adults. Furthermore, the first dorsal fin is slightly notched, a tendency which is much more strongly expressed in a number of other genera. The squamous reduction has progressed about as far as in any member of the family; only the small, simple, tubular, deeply embedded scales of the lateral line remain, and these are curious in being extremely numerous, representing about two scales per body segment instead of one as is usual in the family. The cirri are few in number and most of them are located in places where homologous cirri occur in other genera, but one conspicuous longitudinal cirrus on the median line of the snout is unique within the family and must be accorded some importance in judging the comparatively isolated position of the genus.

Another evolutionary line represented by the genera Jordania and Paricelinus may possibly have stemmed from the ancestor of Scorpaenichthys. These fishes resemble the latter genus and differ from all of the remaining cottids in the retention of five rays in the pelvics and of branched rays in all of the fins. If this be an indication of common origin, the relationship is, nevertheless, remote since they

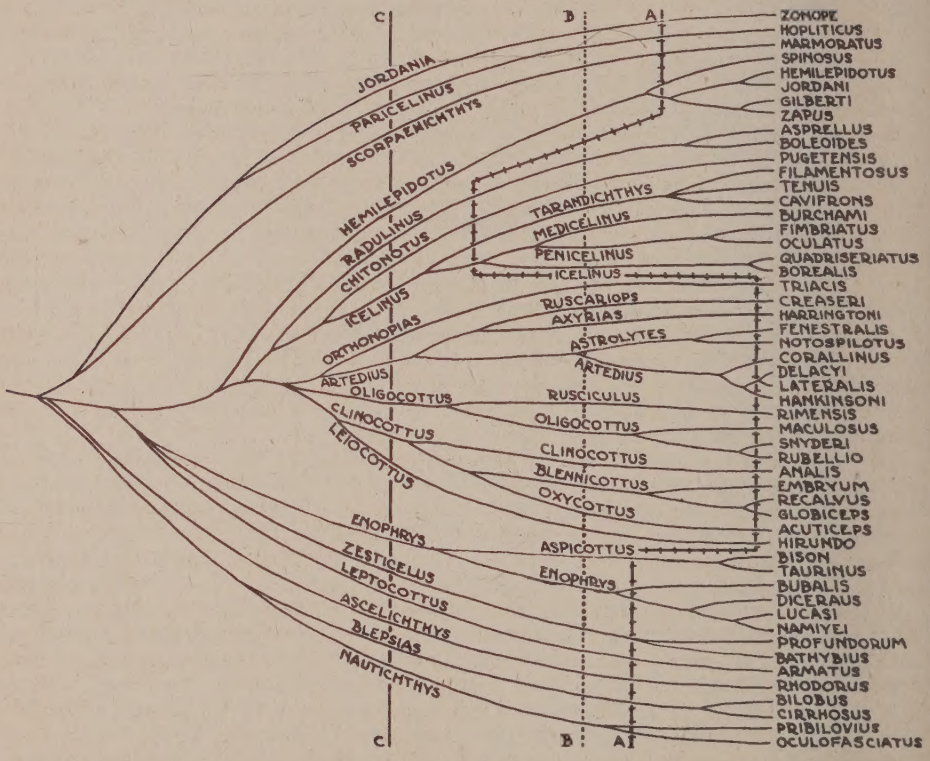

Fig. 1. Phylogenetic tree of the marine Cottidae of California.

differ strongly from Scorpaenichthys in several important respects. The body has become strikingly elongated; the gills are reduced to three and one half; the rather broad membranous connection between the two dorsal fins has been lost and the anal fin has been markedly lengthened so that it is about twice as long as the soft dorsal instead of about equal to it; finally, the body is almost completely scaled.

While Jordania and Paricelinus show undoubted relationship in the similarities noted above, striking differences indicate that they have long existed as genera independent of each other. The minute spinous scales of *Jordania zonope* are arranged in crescentic groups which clearly suggest that they have resulted from fragmentation of large ctenoid scales. Most of those of *Paricelinus hopliticus* are very similar in structure but they show no indication of crescentic arrangement, while one longitudinal series of scales along the base of the dorsal fin has become very much enlarged with each scale bearing a prominent curved spine. In the former fish the preopercular spines are reduced to two; in the latter species three remain and, in addition, spines have been developed on the occiput, along the lower orbit-

al margin and on the suborbital stay which are reminiscent of those found in the scorpaenid genus Sebastolobus and the agonid genus Xeneretmus. In Jordania the first dorsal fin has become somewhat longer than the second dorsal, while in Paricelinus the normal cottid relationship with the second dorsal markedly shorter than the first is retained. These notable differences earn clear generic distinction for these two monotypic lines of development.

An evidently early offshoot from the primitive cottid stock is represented by the genera Blepsias and Nautichthys. These fishes share a few primitive features such as the retention of palatine teeth and of a slit behind the last gill arch, although the gills themselves are reduced to three and one half. The preopercular spines appear to be rather primitive although there is a tendency for reduction of the lower ones. The body has become elongated and compressed instead of depressed as in the majority of cottids. Probably concomitant with the elongation there has occurred a lengthening of the second dorsal and anal fins together with a marked increase in the number of rays, particularly in the dorsal. The pelvic fins have three rays. Minute scales cover most of the body and each of these is deeply embedded and armed with a single spine which is covered by rather heavy skin, so that the fishes appear to be granulated with small dermal papillae. In both forms the anus is advanced to a position far in front of the anal origin. This considerable number of structural similarities clearly indicates the common origin of the two genera but, on the other hand, a number of well marked differences point to a long period of independent existence. Blepsias differs strikingly from Nautichthys in that the gill membranes are not attached to the isthmus, no penis is developed, no branched rays occur in any of the fins (not even in the caudal, which is most unusual) and in being much more compressed. The first two of these characters are conservative, the last two represent modifications of the primitive condition. In Nautichthys only the pelvic fins lack branched rays. Each of these two genera has split into two species. The California representatives, *Blepsias cirrhosus* and *Nautichthys oculofasciatus*, are differentiated from their far eastern congeners, *B. bilobus* and *N. pribilovius*, primarily through differences in proportion and number of rays in the dorsal, anal and pectoral fins.

A group of three California genera, Leptocottus, Zesticelus and Enophrys, have enough characters in common to suggest possible mutual relationship. They all have a body which is very broad anteriorly and displays varying degrees of depression. In all of them the upper preopercular spine is notably enlarged and tends to become branched, the gill membranes are connected to the isthmus, and all scales except those of the lateral line have been lost. A number of other characters are held in common by various pairs of the three genera. For example, Leptocottus and Zesticelus each have only three and one half gills, Leptocottus and Enophrys have retained the slit behind the last gill arch, Zesticelus and Enophrys have lost the palatine dentition. However, the value of all of these characters as indicators of any close mutual relationship is open to serious doubt since each of them is shared with other cottids of widely divergent lines. If the three genera stemmed from a common ancestor they probably diverged at about the same rather remote time.

Leptocottus armatus, the only representative of its genus, retained a comparatively large number of rays in all of the fins, four being present in the pelvics, but all of the rays, except those in the caudal, became simple instead of branched. The preopercular spine became antler-like, with recurved hooks along its upper margin. The reduction of the squamation even affected the lateral line scales which are small, fragile and without spines, and may be considered as obsolescent. An examination of certain osteological details indicates that this form occupies an isolated position. The pelvic bones form a broad-based triangle with the apex di-

rected backward instead of forward and they are attached far laterally on the pectoral girdle instead of medially. The processus medialis of the coracoid is attached to the ala laminaris externa of the cleithrum instead of to the ala laminaris interna. The supraoccipital crest is not so reduced as to be practically lacking, but is well developed and reminiscent of that of the Scorpaenidae, while the suborbital stay falls considerably short of reaching the preopercle and is not directly attached to it. These deep-seated peculiarities contrast strongly with the condition in other cottids that I have had an opportunity to examine in these regards. They suggest that isolation of Leptocottus in a special subfamily might be advisable but, since several forms which might possess the same characteristics have not been available for dissection, it is impossible at present to define the limits of such a category and I prefer simply to call attention to the differences.

The genus Zesticelus is interesting in displaying a stage in which the gill membranes are partially but not fully joined to the isthmus, and by certain modifications induced by the great depths at which it lives, such as the poorly ossified skeleton and the unusually well developed lateral line. The tendency toward branching of the upper preopercular spine is expressed in only one species of the genus, *Zesticelus bathybius*, in which a secondary spine arises from the root of the primary one. Some characters, such as the feeble and deeply embedded scales of the lateral line, the strongly depressed body and the reduced posterior demibranch, hint at relationship to Leptocottus; others, such as the reduced number of rays in the pelvics and the retention of branched rays, in all of the other fins, as well as the loss of the palatine teeth, suggest that it may be related to Enophrys, but the numerous respects in which it differs from each of these genera make it necessary to consider it as constituting still another isolated line of development. It has given rise to only two species, the American *Zesticelus profundorum* and the Japanese *Z. bathybius*, distinguished from the former species by the more extensive development of nasal, occipital and preopercular spines.

The genus Enophrys has been more fertile than any of the others so far discussed and has given rise to several species. Unfortunately, the group as a whole has not been critically studied and it is impossible to state with certainty the exact number of species that it contains. They form a clearly delimited group characterized by the massive head and body, the great size of the upper preopercular spine, the conspicuous sculpturing of the bones of the head, and by the great enlargement and heavy ossification of the lateral-line scales which have developed into massive bony plates.

The ancestral stock evidently split rather early into two distinct developmental lines. One of these, which should be designated as the subgenus Aspicottus, was characterized by a marked tendency toward the reduction of the number of rays in the median fins and by comparative conservatism in regard to the development of bony excrescences on the head, the secondary armature on the upper preopercular spine of adults consisting of small, rounded, bony bosses instead of recurved spines. In this group no penis was developed. The subgenus gave rise to two closely related species, *Enophrys bison* and *E. taurinus*, both occurring in California.

The Pacific representatives of the other main evolutionary line, the subgenus Enophrys, retained a comparatively high number of fin rays in the second dorsal (15 or 16 instead of 9 to 12) and anal (11 or 12 instead of 7 to 9), but in the European *E. bubalis* the number is reduced as in Aspicottus. All of the members of Enophrys developed hooks along the dorsal margin of the upper preopercular spine, and the anal papilla of males lengthened to form a long penis.

The remaining cottids of California fall into a reasonably clear evolutionary pattern. Hemilepidotus is undoubtedly the most primitive genus, retaining a

number of ancestral characters which are reminiscent of Scorpaenichthys. It shares with that genus the body form postulated for the ancestral type, the dorsal fins are still broadly connected by membrane and the notch noted in the first dorsal of Scorpaenichthys is more fully developed. Branched rays occur in all of the fins, even in the pelvics. There are still four gills with a slit behind the last one. Palatine teeth are present, the anus is not advanced and there is no penis. However, this genus differs markedly from Scorpaenichthys in the retention of extensive scaled areas around the base of the dorsal fin, and between the lateral line and anal base, while a narrow streak borders the lateral line dorsally and scattered scales occur in the axilla. The scales of the lateral line itself are numerous and similar in shape to those of Scorpaenichthys, but are decidedly more primitive in bearing a row of rather strong spines along their outer posterior margins. Each of the general body scales is in the form of a flat, deeply embedded plate whose external surface bears a posteriorly inclined, strongly ctenoid, plate-like ridge. They represent a type of scale which is very widespread within the family and from which the more specialized scales could readily have been derived. This genus retains four preopercular spines of primitive form. It has become modified in the reduction of the pelvic rays to four, the initial step in a process which is more advanced in most cottids. The gill membranes have become joined to the isthmus in varying degrees.

This branch of the family tree gave rise to five typical species which fall into three minor developmental lines all displaying about an equal degree of relationship to each other. One of these minor lines is represented by the single species *Hemilepidotus spinosus*, differentiated from its close relatives by a somewhat greater number of dorsal scales and by the fact that the gill membrane forms a very narrow fold across the isthmus or is attached to it by its posterior margin instead of forming a somewhat wider fold. The other four forms, characterized by a somewhat reduced number of dorsal scales and a more extensive fold of the gill membrane, fall into two closely related pairs of species. *H. gilberti* and *H. zapus* are characterized by the fact that in the males the pelvic fins are enlarged and studded with small tubercles or papillae, while in *H. hemilepitotus* and *H. jordani* these fins are unmodified. Aside from these characters, the species are distinguished only by relatively minor differences in body proportions, number of fin rays and color.

The rest of the California Cottidae belong to an evolutionary line which has been extremely malleable and has given rise to several widely divergent genera and numerous species. All of these differ from the ancestral type in having the gills reduced to three and one half and the pelvic rays to three or even to two. In all of them the dorsal fins are entirely separate or practically so, branched rays are never found in the pelvic or pectoral fins, and only in a very few species do they occur singly or in small numbers in the dorsal and anal fins of old specimens. In the various specialized sub-groups so many different morphological features have been modified that no single primitive character is possessed by all of the species to show relationship to any of the genera already discussed. However, certain details of the more primitive members, particularly the scales, indicate that, while these forms undoubtedly did not spring from the modern genus Hemilepidotus, they shared a common and not particularly remote ancestor with the fishes of that genus.

We may assume that the fishes of this fertile evolutionary line split rather early into a deep-water branch and two primarily intertidal branches. The deep-water branch soon split again into two lines. One of these gave rise to the genus Radulinus with the two modern and closely related species *R. asprellus* and *R. boleoides*. Their comparative isolation from the remaining members of the group under

discussion is expressed in their strikingly attenuated body form, the markedly increased number of fin rays in the second dorsal (21 to 23 instead of 12 to 19) and anal (22 to 25 instead of 9 to 16), and in the loss of the palatine dentition. The relationship of these forms to Hemilepidotus is indicated by the structure of the scales which are of the same general type as those found in the latter genus, the undifferentiated body scales being very similar while those of the lateral line differ mainly in the more extensive spination of the outer posterior border and in the greatly increased size. The squamous areas, however, differ from those of all related types. While the genus is primitive in retaining scales on the dorsal surfaces of the head, it is more specialized than its close relatives in having lost almost all of the scales on the dorsal surface of the body; only a thin line of scales persists immediately above the anterior half of the lateral line. It should be noted that in this genus also a small patch of scattered scales in the axilla is characteristic, although these may be entirely missing in some specimens. The genus is further characterized by rather short and simple preopercular spines and by a long, slender, evenly tapered, conical penis in the males.

The remaining portion of the deep-water evolutionary line was characterized by a comparatively stout body, a small number of rays in the median fins, and the retention of teeth on the palatines. It also displayed a tendency to develop a strong cephalic armature which was particularly expressed in the development of the long, antler-like, upper preopercular spine and, to a lesser extent, by the development of sharp postorbital and occipital spines. The scales retained the characteristic hemilepidotid structure. This branch later divided to form the two genera Chitonotus and Icelinus.

The first of these genera is monotypic. Its only species, *Chitonotus pugetensis,* is well characterized by the dense coat of ctenoid scales covering practically the entire dorsal surface of the head and body. The pelvic fins have three rays. The first dorsal fin is so deeply notched that it is often completely divided into two contiguous fins and the anterior spine of this fin is markedly produced. In males the genital papilla has developed into a large cylindrical penis tipped by a blunt curved cone which bears a long recurved flagellum.

Icelinus is distinguished from Chitonotus by the fact that the scales have been entirely lost from the head, those of the dorsal body area have been restricted to a narrow band only two scales in width, the first dorsal is not notched and the pelvic rays have been reduced to two. This genus has given rise to eight species whose mutual relationships have been discussed in a previous paper (Bolin, Copeia 1936, No. 3) but may be reviewed briefly.

Three species, *Icelinus filamentosus, I. tenuis* and *I. cavifrons,* all about equally related to each other, were soon differentiated as the subgenus Tarandichthys, characterized by a tendency to develop filamentous spines in the first dorsal and to retain a few scales in the axilla. The remaining species differentiated further. One branch, the subgenus Icelinus, developed in a manner similar to that of Tarandichthys except for the fin and scale differences just noted and for the reduction of scales on the dorsal surface of the caudal peduncle. This subgenus gave rise to the two closely related species *I. quadriseriatus* and *I. borealis.* The other branch, whose species have pelvic fins of much reduced size, again split into two subgeneric lines: Medicelinus, represented by the single species *I. burchami,* in which the scales are lost from the dorsal surface of the caudal peduncle, no penis is developed, and the skeleton has become fragile and cavernous in response to its deep-water habitat, and Penicelinus characterized by the retention of the peduncular squamation, the development of a penis, and the normal character of the skeleton. This latter subgenus contains two species, *I. fimbriatus* and

I. oculatus.

It is interesting to note that the retention of axillary scales by the three species of the subgenus Tarandichthys duplicates the condition found in the genera Radulinus and Hemilepidotus and indicates the inheritance of the same conservative tendency from a common ancestor, and also that the development of filamentous dorsal rays in Tarandichthys and of a penis in Penicelinus indicates close relationship to the genus Chitonotus.

The remaining two main branches of the phylogenetic tree were marked by a tendency toward reduction of the preopercular spines. The upper spine often became branched but it never elongated or developed into an antler-like structure, while the lower spines became obsolescent and are usually represented by slight angularities of the preopercular border. In the more conservative section of these remaining California cottids scales of the general hemilepidotid type were retained. The scales are arranged in a characteristic pattern but show various stages of reduction in the different forms. Most of the species in this developmental line belong to the genus Artedius which is characterized by the comparatively large head, normal structure of the pelvic fins and by the unadvanced anus. This genus rather early became differentiated into three evolutionary branches. One of these remained primitive in regard to the squamation, the scales forming a dense covering over the dorsal surfaces of the head and extending unbroken over a large portion of the body above the lateral line, even on the dorsal surface of the caudal peduncle. Its conservatism is further expressed by the retention of a small pore behind the last gill, as well as by the comparatively slight reduction of the lower preopercular spines. It is differentiated from most of its more specialized relatives by its very short body and the reduced number of fin rays in the second dorsal (12-14 instead of 14-18) and anal (10 instead of 11-14), and by the possession of a well developed preorbital cirrus. This is the subgenus Ruscariops to which is allocated *Artedius creaseri.*

The second branch gave rise to the subgenus *Axyrias* represented by the single species *Artedius harringtoni.* Its close relationship to the previous subgenus is indicated by the similar squamation which differs mainly in a slight reduction of the scales around the base of the dorsal fins and by the possession of a preorbital cirrus. It is, however, differentiated from Ruscariops by the loss of the pore behind the last gill and by the development of prominent secondary sex characters in the male. These consist of a penis, a great enlargement of the preorbital cirrus, and in the incised membranes of the anal fin being convex instead of concave. While the females of this species could very logically be placed in the same subgenus with *A. creaseri,* the sex-limited modifications must be accorded the same importance as those characteristic of both sexes and subgeneric isolation appears necessary.

The ancestral type of the third branch, which evidently never developed a preorbital cirrus, gave rise to two more very closely related subgeneric lines. One of these, Astrolytes, is characterized by the retention of scales on the head, by the steepness of the snout and by the prominence of the interorbital groove in old specimens. A primitive feature is the usual retention of a few scales just above the axilla. The subgenus contains two species, the comparatively primitive *Artedius fenestralis* which retains a pore behind the last gill and a dense squamation on the dorsal surface of the caudal peduncle, and the more specialized *A. notospilotus* which retains no trace of the last gill slit, has usually lost all of the peduncular squamation and develops a rougher cephalic armature in old adults.

The subgenus Artedius differs from Astrolytes in the loss of scales from both the head and caudal peduncle, by the long, gently sloping snout and by the

flatness of the dorsal surface of the head on which the interorbital groove is little developed. *Artedius corallinus* is the most primitive species, retaining a large number of scales in the dorsal band and even a few just above the axilla. Characterized by the loss of the axillary scales and by a marked reduction in the number of those in the dorsal band are the two closely related and possibly not distinct species *A. lateralis* and *A. delacyi*. In *A. hankinsoni*, the most specialized member of the subgenus, the dorsal scale bands are still further reduced and the upper preopercular spine has become multifid.

The genus Orthonopias, with the single species *O. triacis*, is clearly derived from the Artedius line. The close relationship of the two genera is shown by the same structure and pattern of the teeth, gills and gill membranes, preopercular spines, cirri and scales. The rather compressed instead of depressed body and the extensive cephalic squamation are primitive characters reminiscent of the conservative subgenera Ruscariops and Axyrias rather than the more specialized subgenus Artedius. Three striking characters gain Orthonopias unquestioned generic rank. These are the very much shortened head, the modified pelvic fins which, in the male, have become slightly pedunculate with thickened membrane around the rays and, finally, the advanced position of the anus which is located closer to the pelvic base than to the anal origin.

The remaining California cottids, differentiated from the Artedius series by the obsolescence of the scales which apparently underwent a disintegration or fragmentation as in the genera Jordania and Paricelinus, split again into two evolutionary lines. One of these lines forms the beautifully circumscribed genus Oligocottus in which the anus remained directly in front of the anal origin, the penis became a long, slender and simple cone and the anterior anal rays were modified in the male. In the other line, composed of the genera Clinocottus and Leiocottus, the anus is advanced, the penis heavy and blunt, and the anal fin is unmodified in both sexes.

The interrelationships of the species within the genus Oligocottus seem to be fairly clear. The ancient ancestral type evidently gave rise to two lines of development. One line, the subgenus Rusciculus, was conservative. In it the tendency toward reduction of scales was not strong and almost the entire body remained covered by minute prickles, the preopercular spines remained simple, and the anal fin of the male was not strongly modified. The penis is retractile and few cirri are developed in this line which gave rise to the single species *O. rimensis*.

In the other line of development, the subgenus Oligocottus, all scales except those of the lateral line were completely lost, the preopercular spine expressed a tendency to divide, the anal fin became more modified, the penis developed as a permanently external organ, and the cirri became more numerous. In the most primitive of these species, *Oligocottus maculosus*, the anterior three rays of the anal fin are slightly enlarged and covered by thickened membrane in males. The upper preopercular spine is normally bifid, and the species has shown little tendency toward heavy development of cirri. In *O. snyderi* only the anterior ray of the anal is enlarged in males but the enlargement is great and the first two rays are more or less completely separated from the following ones so that two contiguous or even unconnected anal fins occur. The preopercular spine is similar to that of the previous species and the cirri are somewhat more numerous. *O. rubellio* is the most specialized species. In this form the anterior anal ray of the male is also greatly enlarged and the membrane between the first two rays has become thickened and apparently glandular. While the fin displays a marked notch, the anterior rays have not become separated from the rest of the fin. The preopercular spine has become normally trifid and the cirri more numerous and larger than in other members of the genus.

Of the fishes belonging to the genus Clinocottus, *C. analis* is the most isolated, possessing three characters which serve to distinguish it from all of the others and which require its allocation to its own subgenus. These are the bifid preopercular spine, the retention of small scales similar to those of *Oligocottus reminsis*, and the presence of cirri on the body above the lateral line. In this species there is a marked tendency for a reduction of the palatine teeth which results in their complete absence in some specimens. There is often a slight notch in the first dorsal fin. The penis is in the form of a short blunt cone.

Those members of the genus which have simple preopercular spines, no visible scales and no cirri above the lateral line fall into two groups. One of these, the subgenus Blennicottus, is characterized by a head which becomes rotund and rounded, particularly in adults, by the retention of a pore behind the last gill, and by pelvic fins which show no tendency to be attached to the belly by membrane. *Clinocottus embryum* is the most primitive species, retaining a fairly normal head which becomes rotund only in old specimens, a rather small number of cephalic cirri, and a penis which, although large, is simple and evenly tapered. In the two extremely closely related species, *C. recalvus* and *C. globiceps*, the head becomes hemispherical in shape, the cirri on the head are increased in number and the penis begins to develop a pair of blunt lateral knobs near its tip.

The remaining subgenus, Oxycottus, which contains the single species *Clinocottus acuticeps*, retains the primitive pointed head. The lateral lobes on the penis which were slightly developed in the preceding subgenus have developed into finger-like processes so that the organ has a trifid tip. Furthermore, the pelvic fins have become strongly adnate to the belly and the slit behind the last gill arch has become obsolete.

The final California cottid is *Leiocottus hirundo*, the only species in its genus. Its relationship to Clinocottus is indicated by the structure of the preopercular spines, gills and fins, the loss of scales, the advanced anus and the blunt penis. Its claim to generic distinction must rest primarily upon the gill membranes which are attached to the isthmus near their posterior borders, a character which is not duplicated in any form closer than Hemilepidotus. Corroboratory evidence is provided by the somewhat produced spines of the first dorsal fin and by the lack of palatine teeth. However, both of the latter characters are only more pronounced developments of features that are indicated in Clinocottus and they can not be accorded too great importance.

Having briefly outlined my views on the course of evolution in the California cottids and having expressed these views in the form of a phylogenetic tree, it becomes possible to discuss the logical magnitude of the genera. The extreme left- and right-hand margins of the diagram will admit of little argument. The single stem represents the family Cottidae which is practically universally accepted as including all of the species here depicted. The terminal twigs represent the living species which are recognized in all of the modern literature. I have attempted to depict as accurately as possible the degree of similarity and presumable relationship between the various forms. This degree of relationship is indicated by the position at which the evolutionary lines diverge. Thus the bifurcation which separates *Artedius fenestralis* and *A. notospilotus* is about twice as close to the right-hand border of the diagram as is the split which differentiates both of these species from the *A. corallinus-A. hankinsoni* complex and four times as close as the point of divergence of *A. creaseri* and *A. harringtoni*, which indicates that I consider the first two species to be twice as closely related to each other as they are to the four-species complex, but to be twice as closely related to these

latter fishes as they are to the two species *A. creaseri* and *A. harringtoni*. Some ichthyologists may disagree with me on certain details of the diagram but, since I have attempted to balance each point of divergence in reference to the degree of similarity between the most closely related species on the one hand and the degree of difference between the Cottidae and the remaining families of the order Scleroparei on the other, I believe that I can rely on general acceptance of the figure.

No definite criteria exist for the establishment of generic limits. Systematists have exercised to the full their prerogative of placing these limits where they please. It is probable that no two workers view the problem in exactly the same way; they bring to their task different mental traits and varying points of view. What is a hill to one man is a mountain to another; what is a genus to one man is a group of genera to another. It is the systematist of the latter type who has had the most profound influence on our system of classification, splitting well defined evolutionary groups into a plethora of monotypic genera. These genera tend to persist in the literature since ichthyologists (like most men) seem to regard the printed word as at least semi-sacrosanct. When a generic name has been printed, systematists are much less prone to attempt its suppression than they are to essay the establishment of a new one.

In probing for the reasons which impel generic splitting it may be well to mention one possible factor which I have several times heard mentioned in conversation but have never seen expressed in cold print. This factor is man's vanity. There probably are some individuals who, in the hope that genera bearing their names as authors will grace the publications of centuries to come, rush in with no further basis to establish as many genera as possible. Pride in one's work is to be respected; glory snatching is to be held up to scorn. Such a motive for establishing new genera can hardly be proved and is probably impossible to cure, but workers will do well to base new genera on solid ground in order to avoid suspicion.

Another reason for generic splitting is the striving for nomenclatural stability. When all genera are monotypic the names of organisms can no longer be subjected to changes by further generic splitting. This does provide an argument of sorts for the erection of new genera when new species are established, but it can hardly serve as an excuse for splitting a pre-existing genus since the stability of the original name is thereby destroyed. The cure in this case is the disease itself. Furthermore, it should be clearly understood by all systematists that the genus represents much more than simply one half of the name of an organism. It is a systematic category for the inclusion of related species. It has been this for almost two centuries and reducing its importance by making it synonymous with the species is not an action to be lightly taken.

Most genera are probably split in an attempt to achieve a greater degree of uniformity in the genera than is possible. If we use the genus Clinocottus, sensu lato, as an example we may postulate the disintegration of this group due to the exercise of the splitter's art. It would probably proceed as follows. It is noted that *C. analis* is less closely related to the other members of the genus than these are to each other, or than are the species of the genus Enophrys. It is, therefore, split off to make the remaining genus comparable to Enophrys. Using Zesticelus for comparison, the same type of reasoning results in the isolation of *C. acuticeps* in another monotypic genus. It may then be noticed that the remaining species do not form quite as compact a group as do the species of the genus Radulinus so that *C. embryum* must be removed in a further attempt to achieve uniformity. By this time numerous other genera must be mutilated by splitting in order to conform to the fragments of Clinocottus. A vicious cycle has been set up which can achieve the desired uniformity only when all genera are monotypic and when the genus has lost

all of its systematic significance. It should be clearly realized that while there exists an almost infinite number of varying degrees of similarity between animals, these must be expressed by a very limited number of basic systematic categories: the phylum, class, order, family, genus and species. It is manifestly impossible to have all orders, or all families, or all genera uniform. Different genera will include different numbers of species displaying different degrees of relationship. They can not be strictly comparable and it is futile to attempt to make them so.

Specialists working on particular groups usually seem to be unduly impressed by differences in structure and they often lose sight of the similarities which clamor for recognition as evidences of relationship. On the basis of small and often minute differences they frequently segregate species into smaller and smaller groups. These systematists undoubtedly labor under the impression that they are displaying the interrelationships of the species more clearly. They split a genus of four species into two genera of two species each in order to indicate that two of the species, A and B, are more closely related to each other than they are to C and D, but in doing so they destroy all indication that A, B, C and D are mutually closer to each other than to members of some other genus. Too often, splitting of this type does not represent an increase in knowledge but simply a destruction of all indication of relationship. It should be pointed out that while it is perfectly logical to look upon genera as the units into which a family should be divided, it is equally logical to consider them as the categories into which species should be aggregated. The genus was not established as a category for the purpose of containing a single species unless that species occupies a more isolated position than is usual for the majority of the species within the family.

Whatever the reasons for it have been, it is certain that splitting in most groups of fishes has progressed to the stage in which almost all of the evolutionary emphasis inherent in generic segregation is concentrated at the extreme distal end of the family tree. The line A-A in the diagram indicates the generally accepted limits of the genera of California Cottidae before I began to work on the group. The irregularity in the line is due to the comparatively small amount of work which had been done on the forms from deeper water. Had all forms been investigated as intensively as the more readily available tide-pool species, the generic line would undoubtedly have been an almost straight extension of that portion which lies opposite the Artedius-Oligocottus-Clinocottus complex. If this line be accepted, it appears to be self-evident that the space between the family and the genus has been expanded and that between the genus and species has been reduced beyond all proportion and reason. In the tremendous gap between the family and the genus there are numerous specialized evolutionary lines which represent structural similarities and common ancestry. Since the genus has been displaced far to the right, no basic systematic category is available for emphasizing the importance of these lines. It might be argued that this shortcoming could be solved by reducing the magnitude of the family. This hardly seems advisable since it would result in an enlarged gap between the family and the order which would make it necessary to reduce the higher category. It might also be solved by introducing a new basic category into the gap but, since we can never have enough categories to express perfectly all of the varying degrees of relationship, it seems advisable to rely upon those now in common usage. The logical solution would appear to be the establishment of the generic line at C-C, about midway between the family stem and the specific twigs. If this is done the genus is not vitiated by its encroachment upon the species but stands, as it was originally intended to be, an intermediate category designating the average specialized evolutionary lines within the family.

When families, genera and species have been defined and the magnitude of the

genus has been determined by relating it to the other two categories, it may be advisable to call attention to evolutionary lines of intermediate magnitude by the establishment of other minor categories. These, the subfamilies, tribes and subgenera, should be balanced in the same way as are the basic categories and should not be allowed to modify the magnitude of the latter. The line B-B in the diagram indicates the demarcation line of the subgenera. I have deemed it inadvisable to attempt the designation of subfamilies or tribes, since I consider that this can be done successfully only after the family has been studied on a world-wide basis.

Finally, it may be well to review the systematic history of some of the Cottidae in order to ascertain the basis upon which "genera" have been established. The common tide-pool forms belonging to the genus Clinocottus will serve as suitable material for discussion, since they include species which are very closely related and others which are comparatively strongly differentiated from one another. The genus was established by Gill (Proc. Acad. Nat. Sci. Philadelphia, 1861) in the following words (I quote the entire description): "Clinocottus differs generically from *Oligocottus maculosus* Girard, by the absence of palatine teeth, the presence of prickles on the body, the entire anal fin and the form of the head." This is hardly an adequate generic description by modern standards, but we may grant that the genus is valid and turn to the following original description of Blennicottus which appears on the same page of the same work: "This genus has been also confounded with Oligocottus by Girard, but decidedly differs in the form of the head, its armature, and the structure of the anal fin." Gill was concerned with differentiating Blennicottus from Oligocottus but he made no attempt to compare it with, or to distinguish it from his own newly established Clinocottus. It is, therefore, pertinent to re-examine the characters upon which both Clinocottus and Blennicottus were based, in order to judge whether the latter genus is distinct from the former.

The lack of palatine teeth in Clinocottus might be accorded considerable importance if it were constant. However, in some specimens of the type species, *C. analis*, these teeth are present on both sides, in others they occur on one side only and in some they are totally absent. It seems perfectly self-evident that a character which is not constant among the individuals of a species, or even between the two sides of a single specimen, must be totally valueless for the generic segregation of that particular species.

The presence of prickles on the body seems at first to be much more important, but it must be remembered that these minute scales are structures which, in the cottids, appear to be in the process of reduction. They display the variability so often characteristic of obsolescent organs. Some specimens have extensive scaled areas, others appear to be almost entirely naked, while adults show less prominent squamation than do juveniles. A character of this type should not be accorded too great evolutionary significance. This is particularly true when we note that *Clinocottus recalvus* (and probably *C. globiceps*, the type species of Blennicottus, and *C. embryum* as well, although I have not investigated the latter two species in this regard) does have a few small and deeply embedded scales on the sides of the body above the lateral line. These scales, similar in form to those of *C. analis* are not visible externally and the specimens must be stained with alizarin and cleared before they may be detected. They simply are the few final remnants which represent a somewhat more advanced stage in the reduction of scales which has not progressed so far in *C. analis*. This difference in degree of reduction of obsolescent structures hardly impresses me as being of more than specific importance.

The form of the head was listed by Gill as a character in the establishment of both of his genera. In the type species of Blennicottus it is rotund in the adult and tends to alter the entire general appearance of the fish. For this reason

the character has been greatly stressed. The change is, however, the result of a number of very small proportional changes in several of the cranial bones and neither the general shape nor the relationship of these bones to one another has been altered. Probably the most profound change in the shape of any bone is the one which caused Gill to list the armature of the head as a generic character; the upper preopercular spine is simple in Blennicottus and bifid in Clinocottus. Here we are concerned with a character which is very variable in the closely related genera Oligocottus and Artedius, where it displays a varying number of points in extremely closely related species and often differs on the two sides of the same individual. It should be noted that, in the fishes under discussion, the preopercular spines are becoming obsolete. The process is practically complete in the case of the three lower spines and it is only the upper one which may be designated as a spine at all. Even this one is in the process of reduction and its ontogenetic decline may easily be observed in a series of specimens of the type species of Blennicottus. It is evident that the base of the spine must be the most conservative portion; it can not drop out before the tip does, and any reduction of the tip should certainly be expected to result in the initial reduction of excrescences, in this case the double point. Here, as in the case of the scales, we are concerned with slightly different stages of evolutionary reduction operating on the same organ within the limits of an apparently circumscribed line of evolution. Why minor differences in the shape of bones or parts of bones need be considered of such significance that they must be accorded generic value is beyond my comprehension. We have learned that no two individuals are exactly alike. If we recognize the factor of variability within the species, it would seem logical to consider the genus as a category within whose limits we might expect a somewhat wider range of variation, a range in the shape of a bone from flat to slightly arched or in the shape of a spine from simple to bifid.

Gill's final generic character, the anal fin, needs no comment since it is very similar in the forms under discussion and has never been used as a character in attempting to distinguish them from each other, but only to distinguish them from Oligocottus.

The next genus of the group to be established was Oxycottus, described by Jordan and Evermann, (Bull. U.S. Nat. Mus., No. 47, 1898) as follows: "This genus is allied to Oligocottus, differing in the absence of upward process on the sharp, upwardly curved preopercular spine. No slit behind last gill." Here, again, we are confronted with an inadequate generic description which compares the type with a relatively remote form and ignores any comparison with its closest relatives. An examination of the character of the preopercular spine leads into a repetition of the discussion just completed in the evaluation of the status of Blennicottus. The problem and the conclusion to be reached are exactly the same. The lack of an opening behind the last gill involves another character but apparently its importance should be evaluated in exactly the same way as were the scales and preopercular spines. The last gill slit is an ancient feature which is in the process of being reduced and lost in all of the cottids. Its complete absence in the type species of Oxycottus simply represents the obliteration of an opening which has already been reduced to a small slit or pore in all of its close relatives. Systematists seem to ascribe much greater significance to the difference between a minute pore and none at all than they do to the difference between a minute pore and a large one, while in reality these conditions simply represent stages of approximately equal value along the line of orthogenetic reduction. While the slit is entirely reduced in Oxycottus, its small size in the other members of this restricted evolutionary line impresses me as being an approximation to obliteration and a reason for not

stressing the final closure too strongly.

It should be realized that while the characters so far discussed appear to be of less than generic significance in this particular group of fishes, they are not without value. They are excellent specific characters in most cases and, when coupled with additional features which were not noted by Gill and by Jordan and Evermann, they indicate a degree of differentiation of the forms which may logically be expressed by according subgeneric rank to the three evolutionary lines. On the other hand, when Hubbs (Occas. Papers Mus. Zool., Univ. Mich., No. 94, 1926) described Allocottus and Montereya he used distinguishing characters which appear to be of no more than specific value.

Among the features used by Hubbs to characterize the genus Allocottus we may note that the location of the anus midway between the anal and pelvic fins, the uniform structure of the anal fin in both sexes, "the lateral line with the usual curve," and the nine dorsal spines are equally characteristic of all species of Clinocottus used in its broadest sense. They do not serve to differentiate his genus from its closest relatives. Hubbs lists the penis as being "large and thick, of conic form, without distal processes." It seems to me that here we have a good specific character which represents the second stage in a graded series leading from the comparatively small conic penis of *C. analis* through the enlarged penis of *C. embryum*, which develops slight lateral knobs near the tip in *C. recalvus* and *C. globiceps*, the knobs finally becoming prominent and resulting in a trifid tip in *C. acuticeps*. Instead of using the minor differences to establish monotypic genera, it seems advisable to let the intermediate forms serve to link the species into a common genus. The short, blunt preopercular spines are equally characteristic of Allocottus and *C. recalvus* and *C. globiceps*. The value of slight differences in these spines has already been discussed. The sharp snout and terminal mouth may serve to differentiate Allocottus from *C. recalvus* and *C. globiceps* but not from *C. analis* and *C. acuticeps*. However, this character is not too distinct since, in the subgenus Blennicottus the head tends to become increasingly rotund and the mouth more inferior with advancing age and old specimens of *C. embryum* are very similar to juveniles of *C. recalvus* in these respects. The remaining characters used by Hubbs are the lack of scales and the arrangement of the cirri. The scale problem has already been discussed. The presence or lack of individual cirri seems to be of minor importance when one considers the variation common throughout the family and the fact that a postorbital cirrus, followed by three cirri on the nape and continued by a series of combs along the anterior part of the lateral line, forms an easily recognized basic pattern in all three species of the subgenus Blennicottus.

The characters used to distinguish Montereya from Blennicottus appear to be of even less importance. They all represent slight differences in shape, or degree of development of certain structures. The head is stated to be less bluntly rounded, the snout sharper, the suborbital width equal to or greater than, instead of decidedly less than, the length of the orbit, the mouth barely, instead of decidedly inferior, nasal spine weak instead of moderately strong, preopercular spine barely evident instead of well developed, cirri few and scattered instead of very numerous, etc. Hubbs claims that the fishes differ widely but this point of view is undoubtedly due to his remarkably acute perception of differences. The differences are not nearly as clear as might be supposed from a perusal of his work and even professional ichthyologists, who are previously unacquainted with the two forms, encounter extreme difficulty in the determination of specimens. If these two fishes are to be placed in different genera, then all cottid genera should be monotypic. This is a step which I should contemplate with acute alarm.